Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE VALUE OF CERTAIN NUTRITIVE ELEMENTS IN THE DEVELOPMENT OF THE OAT PLANT

JAMES GEERE DICKSON

INTRODUCTION

It has long been recognized that the incombustible residue resulting from the incineration of a plant is of great importance, and a large amount of work has been done to determine the chemical combinations resulting from the incineration, since by this means it was hoped to determine the nutritive elements which are essential to the plant. This method has proven only partially successful. Liebig (1855), basing his conclusions upon water culture methods, advanced the view that certain salts are indispensable to plant development and maintained that the productiveness of the soil is determined by the essential salts present. Liebig's hypothesis stimulated research, and it was later determined that six ash constituents are essential to the growth of phanerogams, viz., calcium, magnesium, potassium, sulphur, phosphorus, and iron, to which should be added nitrogen, a constituent not found in the ash.

Many similar experiments confirmed these results, but the general trend of investigation soon changed to the study of the function of the elements thus shown to be essential. Various writers, more recently Chirikov (1914) and Truog (1916), have attributed to calcium the function of acting as a carrier of the essential phosphoric acid and as a neutralizer of the organic acids formed in protein synthesis. In agreement with several early workers, Hansteen (1910) has described calcium as functioning in the transformation and transfer of carbohydrates and in the formation of cell walls by green plants. On the other hand, Robert (1911, 1912), confirming the results of earlier investigators, has shown that calcium is not an essential element in the nutrition of fungi, and Molisch (1895) has found that certain algae can thrive without calcium. The effect of calcium in reducing the toxic action of other bases, notably magnesium, in the culture solution has been studied especially by Loeb (1906), Osterhout (1906*a*, 1908, 1911, 1912, 1916), and McCool (1913).

Boehm (1875) was perhaps the first to call attention to some of the specific actions of magnesium salts in culture solutions, and much recent work has demonstrated the toxic action, at least upon green plants, of magnesium salts either alone or when present in excess of a certain ratio to the other bases. It has been shown that magnesium is required for the proper growth of fungi and that, contrary to what occurs in the case of green plants, magnesium may be present in very large quantities without causing a toxic effect. These results have been confirmed by the unpublished work of Mr. J. P. Bennett in this laboratory. This relation of magnesium is in part explained by the fact that magnesium neutralizes the organic acids formed in certain metabolic processes of the fungi and is thus taken out of the field of action. Loew (1892), Bokorny (1895), and Reed (1906) have suggested that magnesium plays an important part in the assimilation of phosphorus and phosphoric acid. It has been found by Sullivan (1905) that certain bacteria can form lipochromes in normal quantity only in the presence of magnesium sulphate and of a phosphate. Others have demonstrated the intimate relation between the presence of magnesium and the formation of vegetable oils, which probably accounts for the high magnesium content of many seeds. Aso (1901) had previously shown by analyses that spores of *Aspergillus oryzae*, which contain a large amount of fat, contain also a moderately large proportion of magnesium.

Nobbe (1870) first pointed out that carbohydrates are formed normally only in the presence of potassium, and Loew (1880) suggested that potassium plays an important rôle in promoting the chemical condensation of proteins, carbohydrates, and fats in plant synthetic processes. Loew's idea is partly based upon Nägeli's (1879) assertion that the potassium salts are better adapted to catalytic work than sodium salts, because of their generally greater affinity for water. It was shown by Schimper (1890) that potassium is essential to the normal development of growing apices. Breazeale (1906) found that plants previously grown in solutions lacking potassium or sodium absorb large quantities of potassium when transferred to a normal nutrient solution containing both these elements.

Early investigations demonstrated that phosphorus is necessary for plant growth and that it occurs chemically combined with many plant substances. Harden (1911) suggested the necessity of phosphorus in fermentation and other enzymatic activities.

More recently thorough studies on the physico-chemical relations existing between the various compounds and elements in culture solutions have been made in an attempt to understand some of the factors neglected in the earlier work. Livingston (1906), Breazeale (1905), Osterhout (1906*b*), Tottingham (1914), and Shive (1915*a*, *b*) have contributed to our knowledge of balanced nutrient solutions.

It has been the purpose of the experiments herein recorded to study the effect of some of the essential nutrient elements upon the development and composition of plants when other physico-chemical factors, such as unequal osmotic pressure and the addition of new chemical elements, were controlled as far as possible.

The culture work from May to August, 1915, and May to August, 1916, was carried on under climatic conditions different from those that governed the latter part of the work, which differences may in some cases explain the differences between the data recorded for the two respective periods. In a later paper a comparison will be made of the meteorological conditions for the two periods.

From September, 1916, to date the work has been carried on in the laboratory of plant physiology at the University of Wisconsin. It is a pleasure to acknowledge my indebtedness to Professor James Bertram Overton for his advice and assistance in supplying the rather extensive apparatus necessary during the course of this investigation.

Methods

Knop's standard nutrient solution, slightly modified by adding 0.1 gram of sodium chloride per liter, which made a salt concentration of 1.5 grams per liter instead of 1.4 grams, was used as the standard nutrient solution throughout the series of experiments. Standard laboratory chemicals were used during the first two years, but on account of the large proportion of impurities, which caused considerable difficulty in the physical study of the solutions and which might also be expected to produce important modifications in the results of the experiments, it was thought best to use the purest chemicals obtainable for all later work. Kahlbaum's analyzed chemicals were finally used, with the exception of potassium nitrate and calcium chloride, of which Merck's "Blue Label" brand was used, and with the exception also of calcium nitrate, which was prepared from a special grade of nitric acid and Iceland spar ($CaCO_3$). All chemicals were reanalyzed for the elements related to the work and calculations were based upon these analyses.

The chemicals were dried at constant temperature until anhydrous or until a definite amount of water remained and then reweighed; distilled water was then added to give the required salt concentration for the stock solutions. In the preparation of the salts it was necessary to make extensive determinations of water content and composition at the various temperatures used in those cases in which no published data for the compound in question could be found. Whenever the methods of other investigators were used they were carefully checked in all cases before being adopted as standards for drying the salts.

Calcium nitrate, potassium nitrate, monopotassium phosphate (Tottingham, 1914), sodium chloride, sodium nitrate, and potassium chloride were dried at 150° C., and weighed as anhydrous. Magnesium sulphate was dried at 160° and treated as containing one molecule of water (Tottingham, 1914). Sodium sulphate was dried at 200° and weighed as anhydrous. Calcium chloride was dried at 200° and treated as containing 0.2 percent water by weight (Weber, 1882). Magnesium nitrate was dried over commercial sulphuric acid (sp. gr. 1.84) and treated as containing two molecules of water. Monosodium phosphate was dried at 100° and weighed as anhydrous. Ferric chloride was weighed without previous drying and considered as containing six molecules of water.

The modified Knop's solution which was used in all the work, as shown in table 1, was of one tenth the concentration described above, and contained, therefore, 0.15 grams total salts per liter instead of 1.5 grams. Previous work has shown that, when wheat and oats are watered during the growing season with the nutrient solution at the higher concentration, the accumulation of salts exerts an inhibiting influence upon their growth.

2.5 cc. of a $M/100$ solution of ferric chloride were added to every liter of culture solution.

The complete cultural series consisted of the "normal" solution, that is, of Knop's solution modified as shown in columns three and four of table 1, and five further modified culture solutions in each of which one of the elements magnesium, calcium, potassium, phosphorus, and nitrogen was reduced to one tenth of the quantity present in the "normal" solution (tables 2 and 3). A quantity of each solution sufficient for the demands of the entire growing season was made up from the stock solutions diluted with water condensed from a block-tin still. The average conductivity of the water at a carbon-dioxide equilibrium with the air was 0.9×10^{-5} reciprocal ohms. The solutions were stored in fifty-liter pure flint glass containers, from which they were drawn when needed.

TABLE 1

The Composition of Knop's Nutritive Solution and of the Modified Knop's Solution Used as the Normal Culture Solution.

Salt	Grams per Liter of Solution		Concentration of Salts Used in Modified Solution	
	Standard Knop's	Modified Knop's	Grams per Liter of Solution	Percentage Composition
$Ca(NO_3)_2$......	0.8	0.8	0.08	0.0533
KNO_3.........	0.2	0.2	0.02	0.0133
KH_2PO_4.......	0.2	0.2	0.02	0.0133
$MgSO_4$........	0.2	0.2	0.02	0.0133
NaCl..........		0.1	0.01	0.0067
Total salt......	1.4	1.5	0.15	0.1000

DISCUSSION OF THE NUTRIENT SOLUTIONS IN TERMS OF CONCENTRATION

Throughout the following discussion concentration will be expressed in terms of percentage of dissolved salts, that is, of grams per 100 cc. of solution, and also in osmotic concentration. The osmotic concentration was calculated upon the basis of electrolytic dissociation as given by Jones (1911, 1912) for all the salts employed except monopotassium phosphate and monosodium phosphate, the data for which are not given in Jones' tables. The electrolytic dissociation of monopotassium phosphate was taken from Tottingham's (1914) table; that of monosodium phosphate was determined by the writer. All measurements were taken at 25° C., which approximates the average temperature of the culture solutions during the growing period. The procedure, as fully described by Tottingham (1914), is based upon the fact that osmotic pressure is a colligative or additive property, depending upon the total number of particles (ions, molecules, and molecular aggregates) in the solution irrespecitve of their kind. An approximation to the total osmotic concentration of any solution may be obtained by summing the values of the partial concentrations of the constituent salts (tables 2 and 3).

TABLE 2

The Composition of the Normal Solution in Terms of Osmotic Concentration

Salt	Dissociation Factor	Concentration			
		Percent	Volume Molecular		
			Decimal	Fraction	Osmotic
$Ca(NO_3)_2$	1.94	0.0533	0.00325	*M*/ 307.7	0.0063
KNO_3	1.90	0.0133	0.00132	*M*/ 758.4	0.0025
KH_2PO_4	1.86	0.0133	0.00098	*M*/1021.8	0.0018
$MgSO_4$	1.87	0.0133	0.00111	*M*/ 903.1	0.0022
NaCl	2.00	0.0067	0.00114	*M*/ 872.5	0.0023
Total salts		0.1000	0.00780	*M*/ 128.2	0.0151

The dissociation of the salts, with the exception of monopotassium phosphate and monosodium phosphate, is considered as occurring in one step in each case as illustrated by the following equations:

$$KNO_3 = K + NO_3,$$
$$MgSO_4 = Mg + SO_4.$$

The two phosphate salts are considered as dissociating in four steps instead of one as shown in the following scheme, which illustrates the complexity of electrolytic dissociation in a solution of monopotassium phosphate, when the process is incomplete and proceeds by stages with increasing dilution.

Stage I. KH_2PO_4.
Stage II. (1) KH_2PO_4, (2) K, (3) H_2PO_4.
Stage III. (1) KH_2PO_4, (2) K, (3) H_2PO_4, (4) H, (5) HPO_4.
Stage IV. (1) KH_2PO_4, (2) K, (3) H_2PO_4, (4) H, (5) HPO_4, (6) H, (7) PO_4.

The algebraical method of calculation of the dissociation of these salts is explained in detail by Tottingham (1914). For practical purposes only the first two dissociation steps indicated above need be considered for monopotassium or monosodium phosphate.

The effects of dissociation in a complex mixture of salts, even when very dilute, are not easily determined. In such a mixture, the influence of one salt upon the dissociation of another should be taken into account in work of this character, but the problem becomes complicated by the difficulties attending calculations. It was not

TABLE 3

The Composition of the Modified Solutions in Terms of Osmotic Concentration

Magnesium 0.1 normal

Salt	Dissociation Factor	Concentration			
		Percent	Volume Molecular		
			Decimal	Fraction	Osmotic
$Ca(NO_3)_2$	1.94	0.0533	0.00325	*M*/ 307.7	0.0063
KNO_3	1.90	0.0133	0.00132	*M*/ 758.4	0.0025
KH_2PO_4	1.86	0.0133	0.00098	*M*/1021.8	0.0018
$MgSO_4$	2.00	0.0013	0.00011	*M*/9031.0	0.0002
Na_2SO_4	1.91	0.0145	0.00102	*M*/ 979.8	0.0019
$NaCl$	2.00	0.0070	0.00119	*M*/ 835.1	0.0024
Total salts		0.1027	0.00787	*M*/ 127.1	0.0151
Calcium 0.1 normal					
$Ca(NO_3)_2$	2.00	0.0053	0.00032	*M*/3077.1	0.0006
KNO_3	1.90	0.0133	0.00132	*M*/ 758.4	0.0025
KH_2PO_4	1.86	0.0133	0.00098	*M*/1021.8	0.0018
$NaNO_3$	1.93	0.0316	0.00371	*M*/ 269.1	0.0072
$Mg(NO_3)_2$	1.99	0.0164	0.00113	*M*/ 904.9	0.0022
Na_2SO_4	1.97	0.0058	0.00041	*M*/2449.5	0.0008
Total salts		0.0857	0.00787	*M*/ 127.1	0.0151
Potassium 0.1 normal					
$Ca(NO_3)_2$	1.94	0.0533	0.00325	*M*/ 307.7	0.0063
KH_2PO_4	1.88	0.0031	0.00023	*M*/5293.6	0.0004
$NaNO_3$	1.97	0.0109	0.00128	*M*/ 779.9	0.0025
NaH_2PO_4	1.91	0.0089	0.00074	*M*/1349.4	0.0014
$MgSO_4$	1.87	0.0133	0.00111	*M*/ 903.1	0.0022
$NaCl$	2.00	0.0067	0.00114	*M*/ 872.5	0.0023
Total salts		0.0962	0.00775	*M*/ 129.0	0.0151
Phosphorus 0.1 normal					
$Ca(NO_3)_2$	1.94	0.0533	0.00325	*M*/ 307.7	0.0063
KNO_3	1.90	0.0133	0.00132	*M*/ 758.4	0.0025
KH_2PO_4	1.94	0.0013	0.00010	*M*/10218.0	0.0002
KCl	2.00	0.0067	0.00090	*M*/ 1112.8	0.0018
$MgSO_4$	1.87	0.0133	0.00111	*M*/ 903.1	0.0022
$NaCl$	2.00	0.0062	0.00104	*M*/ 942.9	0.0021
Total salts		0.0941	0.00772	*M*/ 129.5	0.0151
Nitrogen 0.1 normal					
$Ca(NO_3)_2$	2.00	0.0064	0.00039	*M*/2564.1	0.0008
KH_2PO_4	1.86	0.0133	0.00098	*M*/1021.8	0.0018
KCl	1.99	0.0098	0.00131	*M*/ 760.8	0.0026
$CaCl_2$	1.91	0.0399	0.00359	*M*/ 278.2	0.0068
$MgSO_4$	1.87	0.0133	0.00111	*M*/ 903.1	0.0022
Na_2SO_4	1.97	0.0065	0.00046	*M*/2185.7	0.0009
Total salts		0.0892	0.00784	*M*/ 127.6	0.0151

found practicable, on account of these difficulties, to take into account the effect of one constituent salt upon the dissociation of another in the culture solution, but the degree of dissociation in the various solutions was checked by measurements of electrical conductivity and also by freezing-point determinations.

Samples of the culture solutions for the various measurements were obtained at the termination of the year's experiments. The solutions were thoroughly shaken and filtered through ashless paper without previous wetting of the filter or washing of the residue. The first 500 cc. was discarded and a quantity was then obtained from which samples were taken for all the measurements.

The approximate total amount of soluble salts present in the solutions was determined by evaporating duplicate 10 cc. samples to dryness upon the water-bath. About 0.5 gram of zinc dust was added to each sample as a means of retaining as far as possible the nitric acid which might otherwise be lost on the water-bath and in subsequent drying. The residues were dried at 150° C., cooled in a desiccator, and weighed. The results, corrected for hydrogen evolved, are given in table 4.

The depression of the freezing-point of the different solutions was measured by means of a special Beckman apparatus, care being taken to avoid supercooling below 0.2° C. Readings were obtained that checked within 0.002° C. upon five samples from each solution (table 4).

Electrical conductivity measurements were made of all the solutions with a standard Kohlrausch apparatus. The average conductivity in reciprocal ohms is given in table 4.

TABLE 4

The Amounts of Salts in Solution, Electrical Conductivity, and Depression of the Freezing-Point of the Normal and Modified Nutrient Solutions.

Solution, Deficient Element Given	Total Soluble Salts in Grams per 100 Cc. of Solution			Conductivity × 10^{-5} Reciprocal Ohms			Depression of Freezing-point in Degrees Centigrade.		
	1916 Sol.	1917 Sol.	Ave.	1916 Sol.	1917 Sol.	Ave.	1916 Sol.	1917 Sol.	Ave.
Normal	.110	.105	.107	1.363	1.507	1.435	.050	.051	.050
Mg 0.1		.105			1.556			.051	
Ca 0.1	.085	.070	.077	1.144	1.058	1.101	.050	.050	.050
K 0.1	.109	.082	.095	1.343	1.451	1.397	.050	.051	.050
P 0.1	.098	.090	.094	1.383	1.305	1.344	.050	.051	.050
N 0.1	.120	.109	.114	1.455	1.625	1.540	.050	.061	.055

A comparison of the above tabulated results shows that the concentration of soluble salts is low in the solution in which calcium is deficient and comparatively high in the nitrogen-deficient solution. The lowering of the freezing-point caused by the respective solutions indicates a concentration in each case comparable to that expressed by the total soluble salts, but with less variation. The conductivity measurements, however, express variations in concentration notably similar to those expressed by the soluble salts (table 4 and fig. 1), which fact demonstrates that, at the dilute concentrations used in this work, the conductivity method supplies a very rapid and accurate method of determining the approximate concentration of a culture solution, since at these dilutions hydrolysis and other factors do not appear seriously to affect the conductivity.

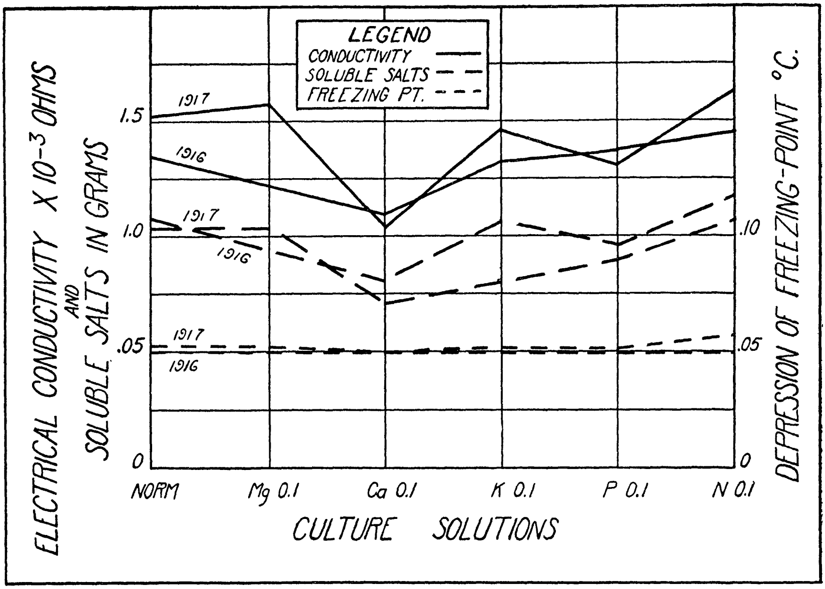

FIGURE 1. Curves showing the amount of salts in solution, electrical conductivity, and depression of the freezing-point in the normal and modified nutrient solutions.

GENERAL CULTURE METHODS

During the years 1915 and 1916 glazed earthenware jars of two-gallon capacity were used for the containers. During the year 1917 jars of four-gallon capacity were substituted for the smaller ones, allowing a greater production of plant substance since the number of plants was increased in proportion to the increase in size of the containers.

The plants were grown in quartz sand, 98 percent of which passed through a sieve of 0.5 mm. mesh. The sand was digested six hours in 10 percent hydrochloric acid and washed free of chlorides with distilled water. The composition of this washed sand was as follows:

SiO_2	99.98%
$FeCl_3$	.014
CaO	trace
K_2O	none
MgO	none
P_2O_5	none

The average moisture-holding capacity of the air-dried sand after the above-described treatment was 25.1 percent by weight.

Each jar was arranged with a four-inch glass funnel inverted in the bottom, into the stem of which was inserted a glass tube of one quarter inch diameter that extended above the top of the jar. A definite amount of sand was then poured around the funnel, after which the jars were covered with heavy paper until they were used for planting.

Pedigreed Swedish select oats, *Avena sativa aristata*, were used in all of the experiments. The seed was sterilized *in vacuo* with 0.25 percent mercuric chloride solution and washed in sterile distilled water until free from chlorides. The method of sterilization was similar to that employed by Hutchinson and Miller (1908), and when plated in bouillon agar after this treatment the seed showed no sign of infection. The seed after sterilization was germinated between cotton towels moistened with sterile distilled water until the primary root protruded beyond the seed coats. The seed was then again washed and planted; three plants were placed in each pot the first season, four the second, and eight the third. The sand in the jars, just previous to the planting of the seedlings, had been brought to 60 percent of its moisture-holding capacity by pouring the culture solution over the surface of the sand, the weight of the jars being recorded. After planting the seedlings, the jars were again covered and allowed to stand until the seedlings appeared above the surface of the sand, when the jars were put on the balance and brought to their former moisture content with distilled water. A small waxed-paper tube was placed around each plant and a paraffin seal run over the top of the moist sand. The tubes were then plugged with cotton to prevent evaporation from the space not occupied by the stem, and the jars were placed in position under the open greenhouse.

The solution in the culture jars was maintained as nearly as possible at 60 percent of the moisture-holding capacity of the sand, the pots being brought to their former weight by pouring the culture solution through the glass tube into the inverted funnel. The jars were aërated by forcing air through this watering tube once a week.

The plants were grown under these conditions until completely matured, a period of about ninety days, from May until August, each year. Frequent observations were made and careful notes taken of the development until the plants were well ripened, when the final data were obtained. In all cases, the essential data are given in the following tables or in the text in connection therewith. The results given in the tables are averages of a series of checks. The number of determinations is given in each instance, with the mean variation following. Peters's abridged method (Briggs and Schantz, 1914), based upon the sum of the departures from the mean, was used to calculate the probable error of the mean as given in the formula

$$Rm = 0.845 \frac{\Sigma d}{n\sqrt{n-1}},$$

in which Rm = the probable error of the mean, Σd the sum of the departures, and n the number of determinations.

THE RELATION BETWEEN NUTRIENTS AND GROWTH

The effect of limiting the essential mineral elements becomes apparent soon after the seedlings are transplanted. The plants grown in the solutions deficient in magnesium or in calcium stool heavily five days before those grown in the normal solutions. Those grown in potassium-deficient solutions, on the other hand, produce plants which stool slightly less heavily than the plants in the normal solutions. Each seedling in the solutions deficient in phosphorus or in nitrogen produces but one slender shoot.

The general appearance of the plants is markedly affected even before stooling begins, and during the subsequent development very characteristic constant modifications are shown. The plants grown in the culture solutions deficient in magnesium develop numerous broad leaves, which are at first very bright green but when older show marked striping as the chlorophyll between the veins disappears.

The plants grown in the culture solutions deficient in calcium develop numerous dark green leaves nearly as long as those of the plants growing in the magnesium-deficient solutions. The lower leaves, however, soon show an inrolling of the margin, a characteristic which Loew (1899) and Tottingham (1914) ascribe to a high magnesium-calcium ratio. Later, at about the time of flowering, brown spots appear upon these inrolled leaves and finally the affected leaves dry and become twisted about the stem. Schimper (1890) describes brown spots on the leaves of Tradescantia grown in the absence of calcium, and von Portheim (1901) notes the appearance of similar spots on the leaves of beans grown in calcium-deficient soils.

The plants grown in the culture solutions deficient in potassium have a smaller total leaf surface than those grown in the normal solutions, but their leaves have very thick dark green laminae. During the period of blossoming, the lower leaves of these plants show long, irregular dark-brown blotches, which appear first near the leaf-base and gradually extend towards the apex.

The plants grown in the culture solutions deficient in phosphorus develop a slender culm which bears a few dwarfed, fleshy leaves. Both the leaves and stems are purplish green, with the purple color apparently gradually replacing the green in the older tissues of the plant. The abnormal coloring appears to be brought about by the presence in the reticulum of the chloroplast of a purple colloidal substance intermixed with the chlorophyll, and resulting perhaps from a progressive decomposition of the latter. Russell (1913) has shown that when barley is grown in phosphorus-free solutions the stems become reddish near the apex.

The plants grown in the solutions weak in nitrogen produce on an average four narrow, yellowish green leaves. Upon microscopic examination, the chloroplasts of these leaves appear to be more or less disorganized.

The period of development is shortened by fully a week when nitrogen or phosphorus is limited, but a deficiency in magnesium or in calcium increases the period of growth about ten days beyond that of the plants grown in the normal solutions.

In general, magnesium- or calcium-deficiency affects least the vegetative development of the plants; in some cases a deficiency in either of these elements causes even an increased growth. In potassium-deficient solutions the growth of the plants is less than that of the plants grown in normal solutions, although the effects are not marked in any particular instance. A deficiency in phosphorus or in nitrogen, however, produces a markedly unfavorable effect upon growth. The relation of the various elements to the general vegetative development of the plants is shown in figure 2.

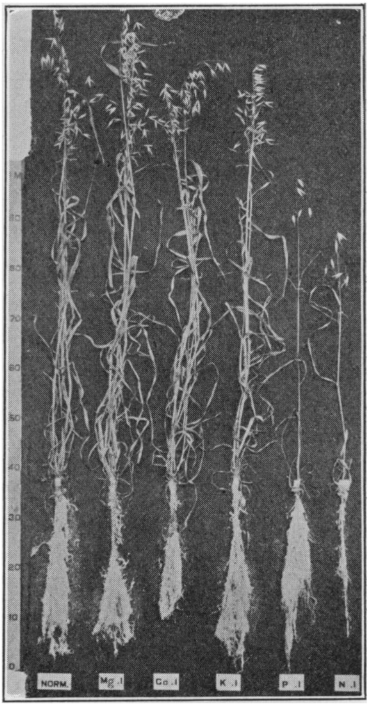

FIGURE 2. ·Photograph showing the growth of oats in the normal solution and in solutions with one essential element in each case reduced to one tenth normal.

THE RELATION BETWEEN NUTRIENTS AND TOTAL DRY WEIGHT

The final vegetative growth and the total dry weight of the plants in the respective cultures at maturity correspond quite closely with the growth of the plants after stooing (at the end of twenty days of growth). Certain specific differences, however, such as the amount of grain produced, the ratio of grain to straw, and the weight of the individual kernels under varying nutritive conditions, are brought out only by carrying the plants to maturity. The plants grown in solutions deficient in magnesium produce a greater total vegetative growth than those grown in normal solutions. The plants grown in solutions deficient in calcium show a total vegetative growth equal to that of plants grown in normal solutions. It is evident, therefore, that if a very small amount of magnesium and calcium is present in the culture solution (one tenth of that in the normal solution), the vegetative development of the plant will not be greatly affected, unless the magnesium-calcium ratio is high enough to exert a toxic effect upon the plant. A deficiency in potassium, however, causes a decrease in the vegetative growth of the oat plant, and also affects the total dry weight which in this case is only about one half that of the plants grown in the normal solution. A deficiency in phosphorus or in nitrogen also causes a very great decrease in vegetative growth. There is no very marked difference in this respect between the effects of a deficiency in phosphorus and those of a deficiency in nitrogen.

TABLE 5

The Average Yields of Dry Weight by Plants Grown in the Normal Solution and in Solutions in Which Certain Essential Nutrients Are Reduced to One Tenth the Normal Amount

No. Det. per Year	Solution, Deficient Element Given	Weight of Dry Matter in Grams			
		1915 Crop	1916 Crop	1917 Crop	Ave.
4	Normal	12.41 ± 1	20.90 ± 2	34.44 ± 0	22.58
2	Mg 0.1			35.42 ± 3	
2	Ca 0.1	13.17 ± 1	23.85 ± 4	24.74 ± 3	20.59
2	K 0.1	6.48 ± 3	15.88 ± 6	15.99 ± 0	12.77
2	P 0.1	2.73 ± 1	1.23 ± 1	2.77 ± 0	2.24
2	N 0.1	4.00 ± 1	.41 ± 0	2.70 ± 0	2.37

The comparative effect of a deficiency in the respective nutrient elements upon the total dry weight of dry matter is presented graphically in figure 3.

THE RELATION BETWEEN NUTRIENTS AND GRAIN PRODUCTION

Although the total dry weight of the plants grown in the solutions deficient in magnesium or in calcium is the same or even greater than that of the plants grown in the normal solution, yet the total dry weight of the grain produced by the plants grown in the former solutions is lower than that produced by plants grown in the normal solution (table 6). The ratio of grain to straw for the plants grown in magnesium- or in calcium-deficient solutions is lower than that of plants grown in the normal solutions. The weight of the individual kernels of the plants grown in the magnesium- or in the calcium-deficient solutions is also below that of the kernels of plants grown in the normal solution (table 7). A deficiency in magnesium or in calcium, therefore, has a markedly deleterious effect upon the grain production of the oat plant.

It is held by some that magnesium or calcium deficiency causes a disturbance in the translocation of carbohydrates and proteins and in their storage during seed formation, rather than an interruption in their synthesis, providing sufficient magnesium is present for the formation of chlorophyll. The results of the experiments reported in the present paper quite substantially support this theory, since the plants in the magnesium- or in the calcium-deficient solutions grow vigorously until the period of seed formation. At the beginning of this phase of their development, however, a deficiency in magnesium or in calcium causes a deleterious effect and results in low grain production.

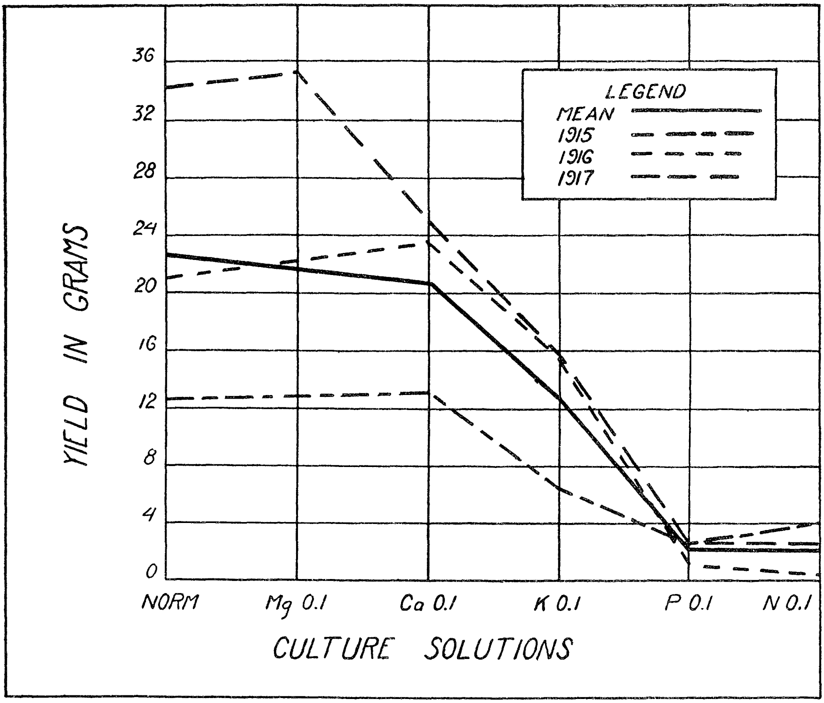

FIGURE 3. Curves showing the average yields of dry matter by plants grown in the normal solution and in solutions in which one nutrient element in each case is reduced to one tenth the normal amount.

A further proof that magnesium functions in some manner in food translocation and storage is that analyses show an abundance of magnesium in the seeds of plants. It has been shown that magnesium occurs chemically combined with many of the fats and some of the phospho-nitrogen compounds. It is possible, therefore, that the major rôle of magnesium in plant nutrition is in connection with seed formation, and if this be true, it is evident that a deficiency in this element in the culture solution will affect seed production rather than vegetative growth. On the other hand, although calcium apparently plays no very important part in the chemical composition of the seed, yet when this element is deficient in the culture solution a marked decrease results in the amount of grain produced. The decrease in the amount of grain produced in calcium-deficient solutions is nearly as great as that noted in magnesium-deficient solutions. It would appear, therefore, that calcium does not function directly in the synthesis of carbohydrates and proteins, but rather as a neutralizer of acids in the plant and as a carrier for nitrogen, phosphorus, and sulphur compounds, a view first advanced by Holzner (1867) and Schimper (1890), and more recently supported by Chirikov (1914) and Robert (1917).

Truog (1916) finds that plants with a high protein content generally have a high calcium content, and that when manganese phosphate is used instead of calcium phosphate as a source of phosphorus the plants grown in such a solution have an extraordinarily high manganese content. Although neither calcium nor manganese is an important constituent of the proteins of the protoplasm, and although neither enters into direct chemical combination with any of the more important compounds of the seed, yet their presence in plants especially high in nitrogen content must indicate some connection with protein formation. In the synthesis of proteins organic acids are formed which must be neutralized by some base to form relatively insoluble salts; calcium, therefore, may be imagined to be the base which chiefly functions in removing these acids from the field of action. From this point of view it would appear that if the nutrient solution is deficient in calcium, and if no other base is present which will form insoluble salts with the organic acids in sufficient quantity to remove the latter, then the normal development of the plant will be disturbed by the accumulation of the acids in sufficient quantities to exert a retarding effect upon the plant's metabolism.

The plants grown in the solutions deficient in potassium produce only about one half the amount of total dry matter produced by the plants grown in the normal solutions. However, the dry weight of the grain produced by the former plants is two thirds of the dry weight of the grain produced by those grown in the normal solutions. The decrease in dry weight of grain resulting from the growing of plants in potassium-deficient solutions is therefore not in proportion to the decrease in the production of total dry matter; for although fewer kernels are formed when plants are grown in potassium-deficient solutions, those that are formed are heavier than an equal number of kernels from plants grown in the normal solutions. Grain formation takes place at the expense of vegetative growth.

The high grain-straw ratio in plants grown in potassium-deficient solutions may be partially explained by tracing the movement of potassium during the development of the plant. Analyses show that potassium is localized first in the growing regions of the young seedling; later, during the development of the flower, it appears in large quantities in the region of grain formation; and finally it is stored in the mature kernel rather than in the straw. As the potassium salts are very soluble, they are readily transferred from the embryonic tissues of leaves and stems to the embryonic region of the flower. Since an abundance of potassium seems to be necessary for meristematic development, the activity of the embryonic regions of the vegetative parts will be checked by the decrease in their potassium supply during flower formation, the result being a high grain-straw ratio.

TABLE 6

The Average Yield of Grain and Straw in Plants Grown in the Normal Solution and in Solutions with One Nutrient Element in Each Case Reduced to One Tenth Normal.

No. Det. per Year	Solution, Deficient Element Given	Weight of Grain in Gm.			Weight of Straw in Gm.		
		1915 Crop	1916 Crop	1917 Crop	1915 Crop	1916 Crop	1917 Crop
4	Normal	5.329 ± 2	6.986 ± 1	6.362 ± 0	7.08 ± 2	14.77 ± 2	28.08 ± 0
2	Mg 0.1			5.804 ± 1			29.62 ± 2
2	Ca 0.1	5.212 ± 1	6.645 ± 0	3.999 ± 0	7.96 ± 2	17.21 ± 3	20.75 ± 2
2	K 0.1	2.968 ± 1	5.660 ± 2	3.268 ± 0	3.51 ± 2	10.22 ± 4	12.68 ± 0
2	P 0.1	1.142 ± 1	.390 ± 1	.665 ± 0	1.59 ± 1	.84 ± 1	2.11 ± 2
2	N 0.1	1.767 ± 1	.120 ± 1	.679 ± 0	2.23 ± 1	.29 ± 0	2.02 ± 0

The general decrease in production of dry matter by plants grown in potassium-deficient solutions may be due to the fact that potassium acts in some way as a condenser or catalyzer in the process of translocation and subsequent condensation of the carbohydrates and proteins. Since phosphorus and nitrogen enter into the chemical composition of compounds found in both foliage and fruit, a deficiency in either of these elements in the culture solution limits the total weight of the grain produced as well as the total dry weight of the plant.

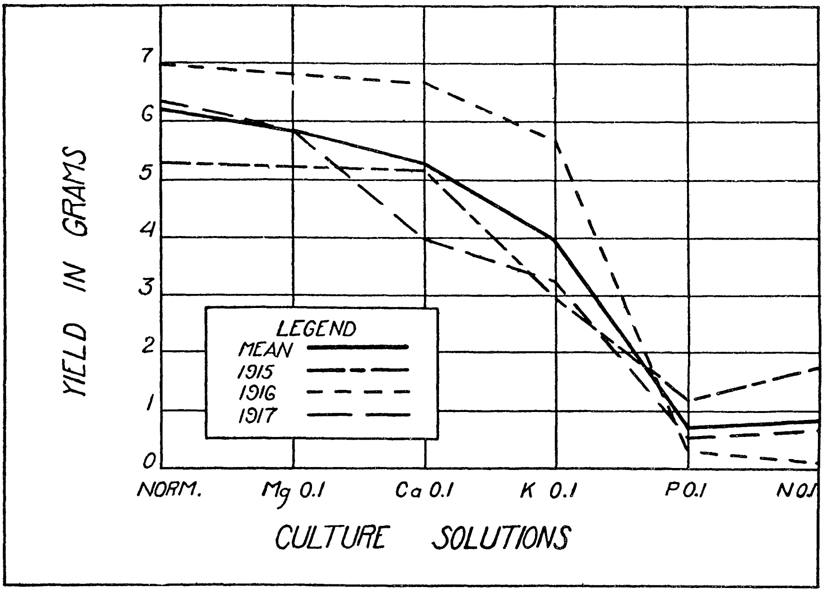

FIGURE 4. Curves showing the average yield of grain by plants grown in the normal solution and in solutions with one nutrient element in each case reduced to one tenth normal.

TABLE 7

The Average Ratio of Grain to Straw and the Weight of the Individual Kernels Produced by Plants Grown in Normal Solution and in Solutions with One Nutrient Element in Each Case Reduced to One Tenth Normal

No. Det. per Year.	Solution, Deficient Element Given	$\frac{\text{Grain}}{\text{Straw}}$ Ratio (in Percentage)				Weights of Individual Kernels in Grams.			
		1915	1916	1917	Ave.	1915	1916	1917	Ave.
4	Normal	75.3	47.3	22.7	48.4	.0204	.0181	.0092	.0159
2	Mg 0.1			19.6				.0081	
2	Ca 0.1	65.5	38.6	19.3	41.1	.0198	.0143	.0089	.0143
2	K 0.1	84.5	55.4	25.8	55.2	.0245	.0175	.0115	.0178
2	P 0.1	71.9	46.4	31.5	50.0	.0238	.0230	.0101	.0190
2	N 0.1	79.3	41.4	33.1	51.3	.0253	.0200	.0186	.0213

Although the ratio of dry weight of grain to dry weight of straw during the three consecutive years varies widely as shown in table 7, yet the effect upon this ratio of a deficiency in any particular nutritive element of the culture solution is similar throughout the three years. The tendency of plants to fruit normally even when their vegetative development is very greatly disturbed is brought out strikingly in the results presented in table 7. Plants grown in magnesium- or in calcium-deficient solutions, provided their vegetative growth is not abnormal, produce an abundance of straw and a relatively small amount of grain. As shown by the weights of the individual kernels in the last four columns of table 7, the grain produced in such solutions is very light. Plants grown in solutions deficient in potassium, phosphorus, or nitrogen, on the other hand, produce a higher ratio of grain to straw, and their kernels are very much heavier than those of plants grown in normal solutions.

Hellriegel and Wilfarth (1888) report that the production of total dry matter and grain are greatly decreased when either potassium, phosphorus, or nitrogen is deficient. Their data show further that the ratio of grain to straw and the weights of the individual kernels of plants grown in solutions deficient in phosphorus or nitrogen are higher than those of plants grown in normal solutions. They record, however, a marked decrease in the ratio of grain to straw and in the weight of the individual kernels in plants grown in solutions deficient in potassium. My own results are at variance with those of some of these experiments, as is shown by the effects of a deficiency in potassium upon the ratio of grain to straw and upon the weight of individual kernels. The data presented in table 7 show that plants grown in solutions deficient in potassium have the highest ratio of grain to straw and that they bear kernels considerably heavier than those of plants grown in normal solutions.

The seasonal variation in the ratio of grain to straw may be partially explained by climatic differences under which the plants were grown for the three seasons. These variations will be discussed in a later paper.

The Relation between Nutrients and Water Requirement

It has long been known that there exists normally a fairly definite ratio between transpiration and growth, and that total transpiration under constant conditions is a more or less accurate criterion of total growth. Many external as well as internal factors, however, influence the rate and amount of transpiration, making the water requirement of any plant very variable. Any particular crop will show a varying water requirement dependent upon temperature, light intensity, concentration of soil solution, and other factors. In a study of the relation of nutrient elements to water requirements, therefore, the necessity is evident of having all other conditions as nearly constant as possible. Great care has been taken in the work here reported to eliminate all environmental variations except the concentration of the mineral nutrients.

In general, a decrease in the normal concentration of the soil solution or in that of any essential nutrient element therein causes an increase in the water requirement of the plants growing upon the soil in question. Hellriegel (1883) finds that the water requirement for oats is doubled by the absence of potassium and trebled by a deficiency in nitrogen. He adds that in general an abnormally high water requirement is to be expected of a plant growing in a soil deficient in any essential element, because growth would be arrested while transpiration would still continue. The experiments herein described and many others of a similar nature show that in general the water requirement of crops is in inverse ratio to the amount of the limiting element in the culture solution.

TABLE 8

The Average Water Requirement, Based Upon the Dry Matter Produced, of Plants Grown in the Normal Solution and in Solutions with One Nutrient Element in Each Case Reduced to One Tenth Normal

No. Det. per Yr.	Solution, Deficient Element Given	Cubic Centimeters of Water Required to Produce a Gram of Dry Matter			
		1915 Crop	1916 Crop	1917 Crop	Average
4	Normal	516 ± 12	440 ± 8	401 ± 2	452
2	Mg 0.1			400 ± 2	
2	Ca 0.1	502 ± 2	407 ± 2	494 ± 1	468
2	K 0.1	614 ± 7	471 ± 2	478 ± 1	521
2	P 0.1	717 ± 5	741 ± 2	832 ± 8	763
2	N 0.1	839 ± 15	1330 ± 14	644 ± 8	938

In this series of experiments, the water requirement, based upon the dry weight of plants at maturity, is enhanced by a decrease in any one of the mineral nutrients with the exception of magnesium (table 8).

The water requirement of the plants grown in the magnesium-deficient solutions is 52 cc. less than the average water requirement of the plants grown in the normal solutions, but the data of one year, 1917, show no perceptible difference between the water requirement of the plants grown in the magnesium-deficient solutions and those in the normal solution. Calcium-deficiency causes a slight increase in the water requirement of the plants when an average of three years' experiments is considered, but in the experiments of the first two years the water requirement of plants grown in the calcium-deficient solutions is less than that of those grown in the normal solution. The average water requirement of plants grown in potassium-deficient solutions is 69 cc. above the water requirement of the plants grown in the normal solution. The water requirement of plants grown in phosphorus-deficient

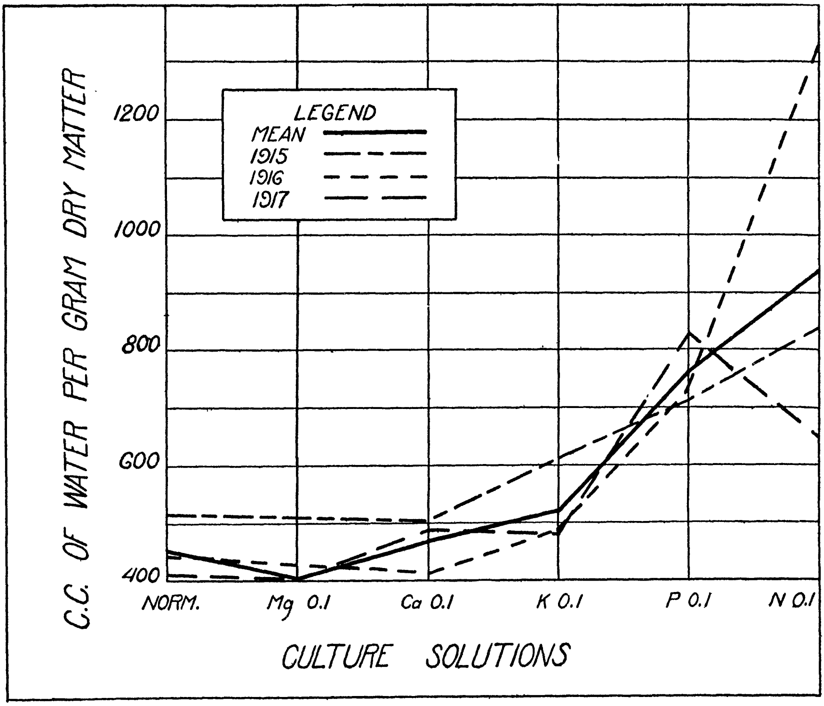

FIGURE 5. Curve showing the average water requirement of plants grown in the normal solution and in solutions with one nutrient element in each case reduced to one tenth normal.

solutions is nearly doubled, and for those grown in nitrogen-deficient solutions it is more than trebled. Figure 5 shows the general relation of the respective nutrient elements to the economic use of water by the oat plant.

SUMMARY

1. The general development of the plants studied is most severely affected by a deficiency in phosphorus or nitrogen.
2. A deficiency in phosphorus or nitrogen prevents the stooling of the plants.
3. The general vigor of growth is increased by a deficiency in magnesium or calcium, and is greatly decreased by a deficiency in phosphorus or nitrogen.
4. The period of development is shortened by a deficiency in potassium, phosphorus, or nitrogen, and is lengthened by a deficiency in magnesium or calcium.
5. The total dry weight of the plants is greater than the normal when magnesium or calcium is deficient, and less than the normal when potassium, phosphorus, or nitrogen is deficient.
6. Grain production is lowered by a deficiency in any one of the elements in question: magnesium, calcium, potassium, phosphorus, and nitrogen.
7. The ratio of grain to straw is decreased by a deficiency in magnesium or calcium, and is increased by a deficiency in potassium, phosphorus, or nitrogen.
8. The weight of the individual kernels is lowered by a deficiency in magnesium or calcium, and is raised by a deficiency in potassium, phosphorus, or nitrogen.
9. The water requirement of the plants is decreased by a deficiency in magnesium, slightly increased by a deficiency in calcium, and greatly increased by a deficiency in potassium, phosphorus, or nitrogen.
10. In general, the effects upon the plants of limiting the supply of phosphorus or nitrogen are much more noticeable than the effects of limiting the supply of magnesium, calcium, or potassium.

DEPARTMENT OF BOTANY,
UNIVERSITY OF WISCONSIN.

LITERATURE CITED

Aso, K. 1901. The Chemical Composition of the Spores of *Aspergillus oryzae.* Bull. Coll. Agr. Tokyo **4**: 81–96.

Boehm, J. 1875. Ueber den vegetabilischen Nahrwerth der Kalksalze. Sitzungsb. Akad. Wiss. Math.-Naturw. Cl. (Wien) **71**: 287–384.

Bokorny, T. 1895. Ueber den Einfluss des Calciums und Magnesiums auf die Ausbildung der Zellorgane. Bot. Centralbl. **62**: 1–4.

Breazeale, J. F. 1905. Effects of the Concentration of the Nutrient Solution upon Wheat Cutures. Science, n. ser. **22**: 146–149.

—— 1906. The Relation of Sodium to Potassium in Soil and Solution Cultures. Journ Amer. Chem. Soc. **28**: 1013–1025.

Briggs, L. J., and **Shantz, H. L.** 1914. Relative Water Requirement of Plants. Journ. Agr. Research **3**: 1–63.

Chirikov, T. W. 1914. Zur Frage über die lösende Wirkung der Wurzeln. Russian Journ. für Exp. Landw. **15**: 54–65.

Hansteen, B. 1910. Über das Verhalten der Kulturpflanzen zu den Bodensalzen. Jahrb. Wiss. Bot. **47**: 289–376.

Harden, A. 1911. Alcoholic Fermentation, pp. 50. London.

Hellriegel, F. H. 1883. Beiträge zu den Naturwissenschaftlichen Grundlagen des Ackerbaus, pp. 622–664.

Hellriegel, H., and **Wilfarth, H.** 1888. Untersuchungen über die Stickstoffnahrung der Gramineen und Leguminoseen. Zeit. Ver. Rubenzucker-Industrie, pp. 1–234.

Holzner, J. 1867. Ueber die physiologische Bedeutung des oxalsäuren Kalkes. Flora **50**: 497–511.

Hutchinson, H. B., and Miller, N. H. J. 1908. Direct Assimilation of Ammonium Salts by Plants. Journ. Agr. Sci. **3**: 179–193.

Jones; H. C., and Hosford, H. H. 1911. The Conductivities, Temperature Coefficients of Conductivity, and Dissociation of Certain Electrolytes. Amer. Chem. Journ. **46**: 240–278.

Jones, H. C. 1912. The Electrical Conductivity, Dissociation, and Temperature Coefficients of Conductivity from Zero to Sixty-five Degrees of Aqueous Solutions of a Number of Salts and Organic Acids. Carnegie Inst. Wash. Publ. 170, pp. 1–143.

Liebig, J. 1855. Die Grundsätze der Agricultur-chemie, pp. 12–13.

Livingston, B. E. 1906. Note on the Relation between Growth of Roots and Tops in Wheat. Bot. Gaz. **41**: 139–143.

Loeb, J. 1906. The Stimulating and Inhibitory Effects of Magnesium and Calcium upon the Rhythmical Contraction of a Jelly-fish (Polyorchis). Journ. Biol. Chem. **1**: 427–436.

Loew, O. 1880. Eine Hypothese über die Bildung des Albumins. Pflüger's Arch. Physiol. **22**: 503–512.

—— 1892. Ueber die physiologischen Functionen der Calcium- und Magnesium-salze im Pflanzenorganismus. Flora **75**: 369–394.

—— 1899. Physiological Rôle of Mineral Nutrients. U. S. Dept. Agr. Div. Physiol. Path. Bull. 18, pp. 1–59.

McCool, M. M. 1913. The Action of Certain Nutrient and Non-nutrient Bases on Plant Growth. Cornell Agr. Exp. Sta. Mem. 2, pp. 121–166.

Molisch, H. 1895. Die Ernährung der Algen. Süsswasseralgen I. Sitzungsb. Akad. Wiss. Math.-Naturw. Cl. (Wien) **104**: 783–800.

—— 1896. Die Ernährung der Algen. Süsswasseralgen II. Sitzungsb. Akad. Wiss. Math.-Naturw. Cl. (Wien) **105**: 633–648.

Nägeli, C. 1879. Ueber die Fettbildung bei den niederen Pilzen. Sitzungsb. Akad. Wiss. München Math.-Phys. Cl. **9**: 287–316.

Nobbe, F., Schröder, J., and Erdmann, R. 1870. Ueber die organische Leistung des Kaliums in der Pflanze. Landw. Versuchsst. **13**: 321–423.

Osterhout, W. J. V. 1906*a*. The Antitoxic Action of Potassium on Magnesium. Univ. Calif. Publ. Bot. **2**: 235–236.

—— 1906*b*. On the Importance of Physiologically Balanced Solutions for Plants. Bot. Gaz. **42**: 127–134.

—— 1908. The Antagonistic Action of Magnesium and Potassium. Bot. Gaz. **45**: 117–124.

—— 1911. The Permeability of Living Cells to Salts in Pure and Balanced Solutions. Science, n. ser. **34**: 187–189.

—— 1912. The Permeability of Protoplasm to Ions and the Theory of Antagonism. Science, n. ser. **35**: 115.

—— 1916. The Penetration of Balanced Solutions and the Theory of Antagonism. Science, n. ser. **44**: 395–396.

von Portheim, L. R. 1901. Über die Notwendigkeit des Kalkes für Keimlinge, insbesondere bei höherer Temperatur. Sitzungsb. Akad. Wiss. Math.-Naturw. Cl. (Wien) **110**: 113–157.

Reed, H. S. 1906. The Value of Certain Mineral Nutrients to the Plant Cell. Annals of Botany **21**: 500–543.

Robert, Thérèse. 1911. Influence du calcium sur le développement et la composition minérale de l'*Aspergillus niger*. Compt. Rend. Acad. Sci. (Paris), **153**: 1175–1177.

—— 1912. Mode de fixation du calcium par l'*Aspergillus niger*. Compt. Rend. Acad. Sci. (Paris) **154**: 1308–1310.

—— 1917. Le rôle physiologique du calcium chez les végétaux. Rev. Gén. Sci. **28**: 101–108.

Russell, E. J. 1913. Soil Conditions and Plant Growth. 2d ed. p. 37.

Schimper, A. F. W. 1890. Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. Flora **73**: 207–278.

Shive, J. W. 1915*a*. A Study of Physiological Balance in Nutrient Media. Physiol. Researches **1**: 327–397.

—— 1915*b*. A Three-salt Nutrient Solution for Plants. Amer. Journ. Bot. **2**: 157–160.

Sullivan, M. X. 1905. Synthetic Culture Media and the Biochemistry of Bacterial Pigments. Journ. Medic. Research **14**: 109–160.

Tottingham, W. E. 1914. A Quantitative Chemical and Physiological Study of Nutrient Solutions for Plant Cultures. Physiol. Researches **1**: 133–245.

Truog, E. 1916. The Utilization of Phosphate by Agricultural Crops, including a New Theory Regarding the Feeding Power of Plants. Wis. Agr. Exp. Sta. Research Bull. 41, pp. 1–50.

Weber, A. 1882. Ueber Chlorcalcium. Ber. Deutsch. Chem. Ges. **15**: 2316–2317.